



Observations of neotropical social wasps (Hymenoptera, Vespidae) preying on eggs and tadpoles of the frog *Engystomops pustulosus* (Amphibia, Leptodactylidae)

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Abstract

In Trinidad, West Indies the social wasps *Angiopolybia pallens* and *Polybia rejecta* come to foam nests of the frog *Engystomops pustulosus*, where they prey on eggs and tadpoles. Frog offspring in early-stage foam nests appear to be almost immune to predation by the wasps, but they become more vulnerable as the nests age and lose definition.

Keywords

Angiopolybia pallens, *Engystomops pustulosus*, *Polybia rejecta*, predation, túngara frog

Introduction

Engystomops pustulosus (= *Physalaemus pustulosus*) (Cope) is a small, nondescript neotropical frog ranging from Mexico to northern South America (Rand 1983). In Trinidad, West Indies, it is one of six leptodactylids that lay their fertilized eggs into viscous foam nests (Murphy et al. 2018). Breeding takes place in very small, shallow, temporary pools.

As the eggs are laid and fertilized, the female secretes a viscous, proteinaceous fluid, which the male beats into a foam with his hindlegs (Breeder 1946; Dalgetty and Kennedy 2010; Heyer and Rand 1977; Ryan 1985), rather like beating egg whites in the kitchen.

This mass of white foam typically floats on the water surface, enveloping the eggs. The tadpoles may remain in the nest for up to five days before breaking through to the water below (Rand 1983). Foam nests of *E. pustulosus* can be distinguished from those of sympatric species in Trinidad by their placement, size and form (Murphy et al. 2018:113–123), so that they almost always can be identified with confidence even in the absence of adult or immature frogs. They disintegrate over time, first becoming flatter and then losing their integrity. The speed of this process evidently varies according to external conditions. For example, heavy rain hastens the process (Ryan 1985).

Adult *E. pustulosus* are taken by a number of predators (Rand 1983; Ryan 1985). Much less is known of the immature stages' natural enemies. The foam nest has no discernible taste (pers. obs.), but it is presumed to provide substantial physical protection to the eggs and the tadpoles as long as these latter remain inside it. Where the larger frog *Agalychnis callidryas* (Cope) is present, its tadpoles often eat *E. pustulosus*'s eggs (Heyer and Muedeking 1976). Once out of the nest, the tadpoles are evidently vulnerable to a variety of predators, including tadpoles of the larger frog *Leptodactylus pentadactylus* (Laurenti) (Heyer and Muedeking 1976). The adults are often preyed upon by the bat *Trachops cirrhosus* (Spix) (Gomes and Reid 2015; Ryan 1985). Among

Angiopolybia pallens (Lepeletier) is a swarm-founding social wasp that ranges from Panama south to Peru and central Brazil (Richards 1978:233). Accordingly, it is broadly sympatric with *E. pustulosus* in northern South America and part of Central America. In Trinidad it is evidently the most abundant social wasp in forests (pers. obs.). Another swarm-founding wasp, *Polybia rejecta* (F.), has a similarly broad distribution (Richards 1978:122), where it is similarly abundant in more open habitats. Both species forage on a broad variety of resources, including carrion (O'Donnell 1995), at which *A. pallens* is especially prevalent (Silveira et al. 2005; pers. obs.). *P. rejecta* is known to prey on the eggs of *A. callidryas* (Warkentin 2000).

Methods

On 12 May 2018 we noticed several female *A. pallens* landing on *E. pustulosus* foam nests in the Arena Forest Reserve (10°33'N, 61°13'W) in central Trinidad. The habitat is mature secondary rain forest on rolling hills watered by many streams. The wasps appeared to be burrowing into the nests to a shallow depth. On 23 May we returned for further observations.

All nests were in potholes in a degraded paved road. For our purposes, it is convenient to recognize three states of the completed nest. In stage 1, the nest is coherent and domed, commonly to 2–4 cm above the water, as when freshly produced (Fig. 1a). In stage 2, it remains coherent but is flattened throughout to no more than 1 cm (Fig. 1b), thereby increasing its surface/volume ratio. And in stage 3 it is distinctly losing its integrity (Fig. 1c).

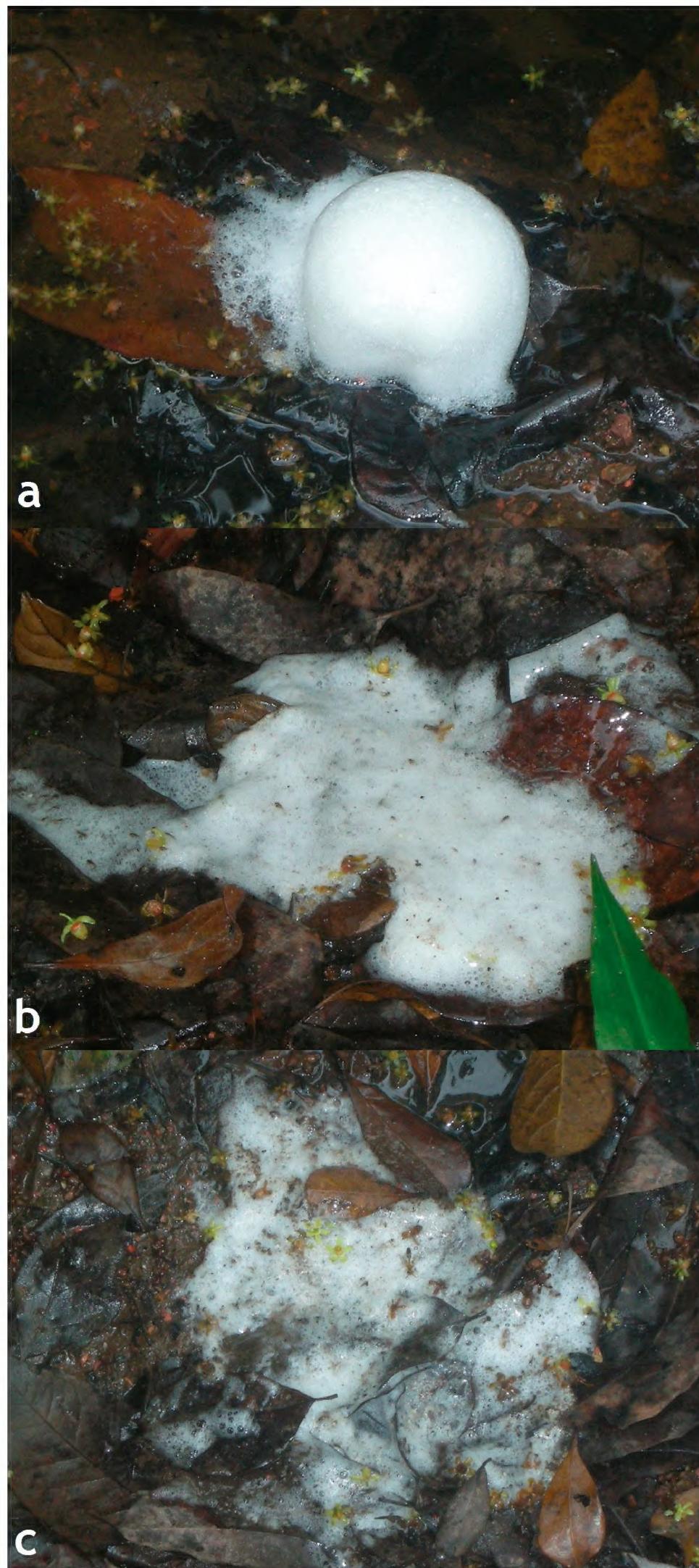


Figure 1. Stages in the disintegration of *Engystomops pustulosus* foam nests. **a** Stage 1; fresh, domed above the water **b** Stage 2; distinctly flatter, but still coherent **c** Stage 3; very flat and losing coherence.

Table 1. Pools in a degraded paved road in Trinidad and their complements of *Engystomops pustulosus* foam nests. See text for explanation of nest stages. One of the stage-2 nests in pool no. 1 was evidently an amalgamation of several original nests from different pairs of frogs.

Pool no.	Stage 1	Stage 2	Stage 3	Wasp visits?
1	4	4	6	+
2	4	4	0	–
3	0	1	0	–
4	1	0	0	–
5	1	1	2	+
6	1	0	0	+
7	0	3	0	+

We made observations at seven pools varying in their composition of foam nests (Table 1). Pool no. 1 was exceptionally large with a surface area of roughly 1 m². At this and several other sites along the road we found wasps landing on the nests. Most of the wasps were *A. pallens*, with only a very few *P. rejecta*, so that all observations below are from the former species except where noted. Our attention was first drawn to several *A. pallens* atop two stage-1 nests at a site with no other nests.

Results

Paring away three stage-1 nests from above, we found abundant dispersed eggs, with the outer 5 or 6 mm free of eggs. Exposed eggs were readily taken by wasps when we stepped away. Some wasps remained to eat the eggs on the spot, while others flew away with them.

Our preliminary observations had been of wasps at a pool with only stage-1 nests. Where nests of different stages were found together, the wasps showed a distinct preference for stage-2 nests (Table 2). This preference is readily explained. Unlike in stage-1 nests, tadpoles were commonly visible just below the surface film of the much flatter nests. They tended to be made even more conspicuous by their movement. Stage-3 nests presumably had nothing to offer except foam.

Wasps often fluttered their wings while walking over the nest surface, possibly as a way of avoiding becoming caught in the surface film. While *A. pallens* commonly burrowed to a depth of its entire head and part of its thorax (Fig. 2), *P. rejecta* hardly penetrated below the surface in our observations. We observed several captures from stage-2 nests, but none by either species from a stage-1 nest except when we exposed eggs.

A few times we saw *P. rejecta* carrying away fragments of foam with no evident egg or tadpole. Lacey (1979) reported *A. pallens* collecting not only eggs and tadpoles but the foam itself from foam nests of *Leptodactylus pentadactylus*. However, in our observations any collection of foam from *E. pustulosus* nests was at most a very occasional activity, not at all like the large numbers of wasps that gather at fresh fruitfalls (pers. obs.). This suggests that nest foam is of only marginal nutritional value and was only taken by wasps that failed in the search for eggs or tadpoles.

Table 2. Wasp landings on *Engystomops pustulosus* foam nests in pool 1. Further explanation in text.

	Stage 1	Stage 2	Stage 3
<i>Angiopolybia pallens</i>	3	50	0
<i>Polybia rejecta</i>	5	15	0

**Figure 2.** *Angiopolybia pallens* burrowing into an *Engystomops pustulosus* foam nest.

Discussion

While characterizing social wasps as “opportunistic, generalist prey foragers”, Raveret-Richter (2000) notes that individuals may return repeatedly to sites of earlier hunting success, making them facultative specialists. *E. pustulosus*’s foam nests are large, very conspicuous (white against the mainly dark forest floor) and stationary. Accordingly, any wasp that has learned to access the abundant eggs and/or tadpoles has good reason to specialize on any nest that she encounters.

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